

## The New Phylogeny of the Lilioid Monocotyledons

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### Abstract

In 1969, Huber radically challenged concepts of familial and ordinal limits of the monocotyledons, emphasizing less conspicuous characters, particularly embryological characters, over gross floral or vegetative morphology. Huber's work highlighted the heterogeneity present in many traditional monocot families, especially Liliaceae. Much of this work was refined and placed into phylogenetic context by the late Rolf Dahlgren and coworkers. In Dahlgren, Clifford, and Yeo's 1985 synthesis, the lilioid monocotyledons are recognized as two orders, the Asparagales, (31 families) and Liliales (10 families) that have evolved many traits in parallel. Two of the most important and consistent characters separating these two orders are the presence of septal nectaries in the ovary and phytomelan in the seed coat of Asparagales. Perigonal nectaries and the absence of phytomelan characterize the Liliales. To date, phylogenetic analyses of the monocotyledons, based on both morphological and multiple gene sequences, have supported this classification with some amendment (for example, Iridaceae and Orchidaceae, classified with Liliales by Dahlgren et al. are now known to belong to Asparagales). The consequence of the phylogenetic approach to classification of the lilies has been the recognition of a sizable number of small families. Most taxonomists believe that classification which reflects true phylogeny is preferable to a synthetic taxonomy that lumps unrelated but convergent taxa into large, unnatural families. The latest research on the new synthesis of monocot evolution is reviewed, with particular emphasis on families rich in horticulturally important geophytic genera, such as Amaryllidaceae, Hyacinthaceae and Liliaceae.

### INTRODUCTION

Phylogenetic analysis (cladistics) has become the standard methodology for testing hypotheses of phylogeny among organisms in systematic biology (Wiley, 1981) based upon principles formally enumerated by Hennig (1966). The main principle of cladistics defines any inclusive group of organisms (a clade), regardless of taxonomic rank, by the presence of one or more shared, derived character states (synapomorphies). Such a group is described as being monophyletic. To accept a taxonomic grouping based on shared primitive character states (plesiomorphies) is not acceptable, and results in polyphyletic (taxonomic groups with multiple evolutionary origins) or paraphyletic groups (groups from which one or more members of common descent are excluded). The further principle of parsimony, the most widely utilized approach in cladistics, states that the shortest possible phylogenetic tree (or cladogram), that is the one that requires the least number of steps (character state changes), is the most accurate. The computer programs used by biologists for cladistic analysis attempt to find the shortest possible (i.e., the most parsimonious) phylogenetic tree produced by a particular character state matrix. Typically, the larger the number of informative (versus neutral or ambiguous) characters in the matrix, the smaller the number of equally parsimonious trees. In the most versatile programs used for this purpose, the researcher can apply various weighting schemes or other assumptions about character evolution to some or all of the data. Several

confidence tests of a particular phylogenetic resolution are employed by systematists, the most widely used being the bootstrap analysis (Felsenstein 1985, 1988; Hillis and Bull 1993; Sanderson 1989). A high bootstrap value for a particular clade is a sign of robustness; a low value means that the clade is not well supported. Cladistics, coupled with molecular approaches to phylogeny reconstruction, has provided quantum leaps in taxonomic science over the past 20 years. Some of the most rapid and radical changes in our understanding of flowering plant phylogeny have been concentrated among the monocotyledons. Illustrative of the speed at which new information is being generated, there have been three major publications on the evolutionary biology and classification of the monocotyledons since 1995 (Rudall et al. 1995; Kubitzki 1998; Wilson and Morrison 2000). Significant changes in our understanding monocot phylogeny have occurred between the release of each.

Huber (1969), who emphasized less conspicuous characters, particularly embryological characters, over gross floral or vegetative morphology, radically challenged concepts of familial and ordinal limits of the monocotyledons. Huber's work highlighted the heterogeneity present in many traditional monocot families, especially Liliaceae Juss. Much of this work was refined and placed into phylogenetic context by Dahlgren and coworkers (Dahlgren and Clifford 1982; Dahlgren and Rasmussen 1983; Dahlgren, Clifford, and Yeo 1985). In Dahlgren et al.'s (1985) synthesis, superorder Liliiflorae encompasses 5 orders: Dioscoreales, Asparagales, Melanthiales, Burmanniales and Liliales. To date, phylogenetic analyses of the monocotyledons, based on both morphological and gene sequence matrices, have supported this classification with some amendment (Duvall et al. 1993; Stevenson and Loconte 1995; Chase et al. 1995a, b, 2000).

Most notably, Melanthiales is no longer recognized as distinct from Liliales [Angiosperm Phylogeny Group (APG) 1998], Burmanniales is placed within Dioscoreales (Caddick et al. 2000), and Iridaceae Juss. and Orchidaceae Juss. have been transferred from Liliales to Asparagales, primarily on the basis of DNA sequence data (Chase et al. 1995a, 2000). The most recent analysis of molecular data (Chase et al. 2000) across all of the monocotyledons utilized a combined matrix of three genes: plastid *rbcL*, plastid *atpB* and nuclear 18S ribosomal DNA (Fig. 1). The results of these and other analyses has resulted in a formal reclassification of the flowering plants along a strict criterion of monophyly, published by the Angiosperm Phylogeny Group (APG 1998), and it is this latter system that will be utilized as a framework for the discussion in this paper.

In Dahlgren et al.'s (1985) synthesis, based on Huber's (1969) seminal work, the families of monocots rich in geophytes are classified into two orders, Asparagales and Liliales, that have evolved many traits in parallel. Dahlgren et al. (1985) listed 16 characters that differentiated Liliales and Asparagales, but most do not occur in all taxa and several at least are plesiomorphic states. The two important and consistent characters that separate the two orders are the presence of phytomelan in the seed coat of Asparagales (Huber, 1969), and the universal absence of septal nectaries in Liliales (Rudall et al. 2000). As Dahlgren et al. (1985) and Goldblatt (1995) point out, the boundaries between the two orders are difficult to define on morphological grounds alone, though multiple gene sequences support these two orders as monophyletic groups (Chase et al. 2000).

## LILIALES

Dahlgren et al. (1985) originally recognized ten families in Liliales: Alstromeriaceae Dumort., Colchicaceae DC., Uvulariaceae Kunth, Calachortaceae Dumort, Liliaceae, Geosiridaceae Jonker, Iridaceae, Apostasiaceae Lindl., Cyripediaceae Lindl. and Orchidaceae. Plastid DNA sequences have since resulted in Iridaceae (including Geosidridaceae) and Orchidaceae (including Apostasiaceae and Cyripediaceae) being transferred to Asparagales (Chase et al. 1995a). The most current classification (APG, 1998) recognizes the following nine families: Alstromeriaceae, Campynemataceae Dumort, Colchicaceae, Liliaceae, Luzuriagaceae Kunth,

Melanthiaceae Batsch, Philesiaceae Dumort, Ripogonaceae , and Smilacaceae Vent. Rudall et al. (2000) suggest combining Philesiaceae and Ripogonaceae with Smilacaceae (Fig. 2).

Cladistic analyses of combined plastid genes *rbcL* and *trnL-F* resolves four main lineages within the Liliales (Fig. 2; Rudall et al. 2000): 1) Liliaceae (including Calochortaceae and some former members of Uvulariaceae), Philesiaceae, and Smilacaceae; 2) Campynemataceae; 3) the colchicoid lilies (Colchicaceae including *Petermannia* F. Muell. and *Uvularia* L.), Alstroemeriaceae and *Luzuriaga* R. & P.; and 4) Melanthiaceae (including Trilliaceae Lindl.). The relationships between these lineages are not well resolved. A cladistic analysis using morphological characters provides much less resolution among and within these groups (Rudall et al., 2000), while a combined analysis yields a tree topology similar to the molecular data alone, with the exception of the position of *Calochortus* Pursh. (Fig. 2).

*Liliaceae*. In the latest synthesis of Rudall et al. (2000), Liliaceae sensu stricto appear to consist of two main groups (Fig. 2). The larger clade based on plastid sequences is made up of three subclades (all genera not listed): 1) a *Clintonia* Raf.-*Gagea* Salisb. clade; 2) the core Liliaceae (*Lilium* L., *Fritillaria* L., *Nomocharis* Franch., *Cardiocrinum* Endl.), and 3) a *Tulipa* L.-*Erythronium* L. group. The smaller main clade represents part of what Dahlgren et al. (1985) treated as Uvulariaceae (*Tricyrtis* Wall. and allies). *Calochortus* is sister to Liliaceae in the *rbcL/trnL-F* trees, but is embedded between the two main clades of the family in the combined analyses presented by Rudall et al. (2000; Fig. 2). Patterson et al. (1998), using the more rapidly evolving chloroplast gene *ndhF*, resolved *Calochortus* as sister to *Tricyrtis*. Tamura (1998a) recognized Calochortaceae, isolating *Calochortus* in the monogeneric bulbous tribe Calochortae Melchior. The remaining four rhizomatous genera (including *Tricyrtis*) were placed in the tribe Tricyrtideae K. Krause. Liliaceae as narrowly circumscribed, is a predominantly holarctic family (Tamura 1998b).

*Colchicaceae*. This cormous and rhizomatous family includes the horticultural genera *Gloriosa* L., *Sandersonia* Hook., *Littonia* Hook., and *Colchicum* L. and five other genera (Nordenstam 1998), including *Uvularia*, the only North American genus of the family.

*Melanthiaceae*. The taxonomic history of this group of lilies has been problematic, to say the least (Zomlefer 1997), but appears to be well defined morphologically by extrorse anthers and three styles (again, these characters occur elsewhere in Liliales). Tamura (1998c) did not include Trilliaceae (Zomlefer 1996; Tamura 1998d) in his treatment. Trilliaceae resolves as embedded within Melanthiaceae in many molecular analyses (Rudall et al. 2000).

*Alstroemeriaceae*. This New World endemic family generally resolves as an isolated lineage most closely related to the genus *Luzuriaga* and a monophyletic Colchicaceae (Chase et al. 1995a, 2000; Rudall et al. 2000). Bayer (1998) recognized five genera: *Alstroemeria* L., *Bomarea* Mirb., *Leontochir* Phil., *Schickendantzia* Pax, and *Taltalia* Her. Bayer. The latter two genera are segregates from *Alstroemeria* and are not supported by cladistic analyses of chloroplast DNA variation (Aagesen and Santo 1998). In Aagesen and Santo's (1998) analysis, *Bomarea* and *Leontochir* are sister genera, and the Andean species of *Alstroemeria* are embedded within the Brazilian species of the genus.

## ASPARAGALES

Thirty-one families were included in Asparagales by Dahlgren et al. (1985). Analyses of *rbcL* sequence data (Chase et al. 1995a) resulted in the transfer of Orchidaceae and Iridaceae from Liliales (Dahlgren et al. 1985) to Asparagales. Conversely, several families treated by Dahlgren et al. (1985) within Asparagales have been moved to Liliales. The Angiosperm Phylogeny Group recognizes 29 families in the order (AGP, 1998).

Asparagales consistently forms two groups, a clade of what has been termed the

“lower” asparagoids (characterized by a predominance of simultaneous microsporogenesis and frequently inferior ovaries), and a clade of “higher” asparagoids with uniformly successive microsporogenesis and frequent occurrence of superior ovaries (Rudall et al., 1997). Relationships between the families within each group have unfortunately presented problems (Chase et al. 1995a), and macromorphological synapomorphies for many of the families are not apparent (Fay et al. 2000). Fay et al. (2000) presented analyses of four plastid sequence data sets that produced trees largely congruent with the *rbcL* topology of Chase et al. (1995a), but with increased bootstrap support for many of relationships resolved among the families (Fig. 3). The higher asparagoids, Amaryllidaceae J. St.-Hill. and Alliaceae J. Agardh form a sister relationship with Agapanthaceae Voigt sister to both. Analysis of plastid sequences alone place Alliaceae as sister to an Agapanthaceae/Amaryllidaceae clade (Fay and Chase 1996; Meerow et al. 1999). Themidaceae Salisb. (the former tribe Brodiaeae of Alliaceae) is allied with Hyacinthaceae Batsch and Aphyllanthaceae Burnett. Agavaceae Endl. is included in a clade with Anthericaceae J. Agardh. and several smaller families. Hemerocallidaceae R. Br. forms a clade with Asphodelaceae Juss. and Xanthorrhoeaceae Dumort. Convallariaceae Horan. is united with Asparagaceae and Laxmanniaceae. Iridaceae resolves in an isolated position near base of the higher asparagoids, while Orchidaceae is in the basalmost position relative to all the asparagoids.

*Alliaceae.* Fay and Chase (1996), on the basis of a phylogenetic analysis of *rbcL* sequence data, removed *Agapanthus* L' Hér. from Alliaceae, and resurrected the family Themidaceae for the western North American and Mexican genera of Alliaceae (tribe Brodiaeae). In Fay and Chase's (1996) *rbcL* trees, Alliaceae forms two subclades: 1) an American/South African group (*Tulbaghia* L. is the only endemic African genus of the family) and 2) an *Allium* L./*Milula* Prain clade. *Tulbaghia* is sister to the endemic American genera of the family. Meerow et al.'s (1999) combined plastid sequence analysis (Fig. 4) supported this resolution of Alliaceae, though in trees resulting from the *trnL-F* matrix alone, *Tulbaghia* is sister to the rest of the family. Fay and Chase (1996) proposed three subfamilies, Allioideae (*Allium* and *Miulla*), Tulbaghioideae (*Tulbaghia*) and Gilliesioideae (for all endemic American genera, e.g., *Leucrocoryne* Lindl., *Iphieon* Raf.). In Rahn's (1998) treatment, 13 genera are recognized.

*Amaryllidaceae.* Amaryllidaceae is one of the few families of Asparagles well-defined by other than molecular characters, namely umbellate cymes, inferior ovaries, and unique alkaloid chemistry (Meerow and Snijman, 1998). The four most recent infrafamilial classifications of Amaryllidaceae are those of Traub (1963), Dahlgren et al. (1985), Müller-Doblies and Müller-Doblies (1996) and Meerow and Snijman (1998). Traub's scheme included Alliaceae, Hemerocallidaceae and Ixioliriaceae as subfamilies, following Hutchinson (1934, 1959) in part. Within his subfamily Amarylloideae, he erected two informal taxa, "infra-families" Amarylloidineae and Pancratioidineae, both of which were polyphyletic (Meerow, 1995). Dahlgren et al. (1985) dispensed with any subfamilial classification above the level of tribe, recognizing eight, and treated as Amaryllidaceae only those genera in Traub's Amarylloideae. Stenomessae Traub and Eustephieae (Pax) Hutch. were combined. Meerow (1995) resurrected Eustephieae from Stenomessae and suggested that two new tribes might need to be recognized, Calostemmatae D. & M-D. and Hymenocallideae (D. & U. M-D.) Meerow. Müller-Doblies and Müller-Doblies (1996) recognized ten tribes (among them Calostemmatae) and nineteen subtribes, many of them monogeneric; Meerow and Snijman (1998) recognized 13 tribes, with two subtribes only in one of them. A discussion of character evolution within the family can be found in Meerow (1995) and Meerow et al. (1999).

Fay and Chase (1996), on the basis of a phylogenetic analysis of *rbcL* sequence data, recircumscribed Amaryllidaceae to include *Agapanthus*, previously included in Alliaceae, as subfamily Agapanthoideae. All the epigynous genera (Amaryllidaceae *sensu stricto*) were treated as Amaryllidaceae subfamily Amaryllidoideae. Bootstrap support for the sister relationship of *Agapanthus* and Amaryllidaceae was weak (63%). Moreover, the sampling within Amaryllidaceae s.s. (only 4 genera) in Fay and Chase (1996) did not

allow sufficient resolution of the generic relationships within the family. Meerow et al. (1999) presented cladistic analyses of plastid DNA sequences *rbcL* and *trnL-F* alone and in combination for 51 genera of Amaryllidaceae and 31 genera of related asparagalean families. The combined analysis was the most highly resolved of the three (Fig. 4) and provided good support for the monophyly of Amaryllidaceae and indicated Agapanthaceae as its sister family (though bootstrap support for this relationship was still weak at 60%). Alliaceae were in turn sister to the Amaryllidaceae/Agapanthaceae clade. In Fay et al.'s (2000) four gene analysis, Agapanthaceae is sister to Amaryllidaceae/Alliaceae. Based on these data, it would be possible to argue for recognizing Amaryllidaceae in a modified Hutchinsonian (1934) sense, i.e., with three subfamilies, Allioideae, Agapanthoideae, Amarylloideae. However, there is no distinctive morphological synapomorphy for this treatment. Meerow et al. (1999) opted to recognize a monotypic Agapanthaceae, which has been adopted by the Angiosperm Phylogeny Group (AGP, 1998).

Based on the cladistic relationships, the family originated in western Gondwanaland (Africa), and infra-familial relationships are resolved along biogeographic lines (Fig. 4). Tribe Amaryllideae J. St.-Hil., entirely southern African with the exception of pantropical *Crinum*, was sister to the rest of Amaryllidaceae with very high bootstrap support. The remaining two African tribes of the family, Haemantheae (Pax) Hutch. (including Gethyllideae Dumort) and Cyrtantheae Salisb., were well supported, but their position relative to the Australasian Calostemmatae and a large clade comprising the Eurasian and American genera, was not clear. Most surprising, the Eurasian and American elements of the family were each monophyletic sister clades. Internal resolution of the Eurasian clade only partially supported currently accepted tribal concepts and few conclusions could be drawn on the relationships of the genera based on these data. A monophyletic Lycorideae Traub (Central and East Asian) were weakly supported. *Galanthus* L. and *Leucojum* L. (Galantheae Salisb. pro parte) were supported as sister genera by the bootstrap. The American clade showed a higher degree of internal resolution. Hippeastreae (Pax & Hoffm.) Hutch. (minus the unresolved *Griffinia* Ker-Gawl. and *Worsleya* Traub) were well supported, and a distinct subtribe Zephyranthinae was resolved as well. A distinct Andean clade marked by a chromosome number of  $2n = 46$  (and derivatives thereof) was resolved with weak support. Within the Andean group, a petiolate subclade resolved in the *rbcL* phylogenies, but not in the *trnL-F* or combined analysis. Five recognized tribes of Amaryllidaceae are consistently resolved by the plastid DNA sequences, and all receive strong bootstrap support (Fig. 3). These are the Amaryllideae, Haemantheae, Calostemmatae, Galantheae and Hippeastreae. Lycorideae is also resolved, but without support.

Ito et al. (1999) resolved a very similar topology for a more limited sampling of Amaryllidaceae and related asparagoids using plastid *matK* sequences, but *Agapanthus* was sister to a diverse clade of Agavaceae, Anthericaceae, Hostaceae B. Mathew and Hyacinthaceae in their trees, the former three families represented by a single species each. There was no bootstrap support for this position of *Agapanthus* in their analyses.

Meerow et al. (2000a, b) analyzed 77 species of the monophyletic American Amaryllidaceae using the internal transcribed spacer (ITS) of nuclear ribosomal DNA *Pancratium* L. as outgroup (from the Eurasian sister group to the American clade in plastid DNA analyses; Meerow et al., 1999). This resulted in a highly resolved phylogeny with relatively few unresolved branches (Fig. 5). The American genera of the family form two major subclades. The first, or "hippeastroid" clade, could be described as the diploid ( $n = 11$ ), primarily extra-Andean element of the family (though several of the genera do have Andean representatives), comprising the genera treated as the tribe Hippeastreae in most recent classifications (Dahlgren et al. 1985, Müller-Doblies and Müller-Doblies 1996; Meerow and Snijman 1998). The second subclade constitutes the tetraploid-derived ( $n = 23$ ), Andean-centered tribes. Moreover, the Andean subclade is characterized by 3 consistent deletions, two in the ITS1 and one in the ITS2 regions. Several genera within the hippeastroid subclade resolve as polyphyletic (*Rhodophiala* Presl., *Zephyranthes*

Herb.), and the possibility of reticulate evolution (i.e., early hybridization) in these lineages was hypothesized (Meerow et al. 2000b). In the Andean clade, a petiolate-leaved clade containing elements of both Eucharideae (Pax) Hutch. and Stenomesseae was resolved with a bootstrap = 93%. In both of the American subclades, there is a small tribe that is sister to the rest of the subclade, the Eustephieae in the Andean group, and the Griffineae Rav. in the hippeastroid clade. These two small tribes may represent either ancestral or merely very isolated elements of their respective clades.

In a survey of internal morphology of American and African Amaryllidaceae, Arroyo and Cutler (1984) noted several characters that separated American genera from African. All American species surveyed have scapes with collenchyma, a one-layered rhizodermis, and obvolvate bracts. All Amaryllideae (entirely African with the exception of pantropical *Crinum* L.) have schlerenchyma in the scape, a multi-layered rhizodermis, and equitant bracts. *Haemanthus* L. and *Cyrtanthus* Aiton exhibit scape and root anatomy of the American species, but the equitant bracts of Amaryllideae (Arroyo and Cutler 1984). Calostemmateae (*Calostemma* R. Br. and *Proiphys* Herb.), which were not discussed by Arroyo and Cutler (1984), have equitant bracts. Many of the Eurasian genera have fused spathe bracts which obscures the pattern of their coherence, but both *Lycoris* Herb. and *Pancratium* species with free bracts show the equitant condition. *Worsleya* is the only American genus with the equitant bract condition of the Old World genera, suggesting that Griffineae may represent one of the more ancient American lineages in the family.

*Convallariaceae*. This family sensu Dahlgren et al. (1985) are rhizomatous perennial herbs with a primarily northern hemisphere distribution. They are particularly abundant in eastern Asia. Three tribes are recognized: Polygonateae Benth., Ophiopogoneae Endl., and Convallarieae (Conran and Tamura 1998). Some workers recognize a fourth, Aspidistreae (Dahlgren et al. 1985). The seeds of the berry fruits lack phytomelan. The *rbcL* analysis of Chase et al. (1995a) suggested that the Ophiopogoneae should be allied with Ruscaceae Spreng. ex Hutch. and Asparagaceae Juss. Rudall et al.'s (1997) analysis of *rbcL* sequences indicated that Convallariaceae were polyphyletic, and intergrade with Nolinaceae Nakai, Dracaenaceae Salisb. and Ruscaceae, all families of woody plants. Yamashita and Tamura (2000) used the plastid gene *tmK* (inclusive of *matK*), along with *rbcL* to investigate the same problem, and were not able to resolve a monophyletic Convallariaceae. However, the tribes Polygonateae and Ophiopogoneae were resolved as monophyletic, and the Convallarieae and Aspidistreae formed a clade, results contrary to Rudall et al.'s (1997) conclusions. The Angiosperm Phylogeny Group (AGP 1998) included Nolinaceae, Dracaenaceae and Ruscaceae within Convallariaceae. Clearly, a consensus on the interrelationships of the non-phytomelanous asparagoids is still elusive. In Fay et al.'s (2000; Fig. 3) multiple sequence analysis, Convallariaceae forms a clade with Asparagaceae and the Laxmanniaceae (formerly Lomandraceae Lotsy).

*Hemerocallidaceae*. The modern consensus on this morphologically diverse family (Clifford et al. 1998) unites the daylilies (*Hemerocallis* L.) with New Zealand flax (*Phormium* J. R. Forst. & G. Forst.) and 11 other genera, including *Dianella* Lam. Ex Juss. Though previously treated as a monogeneric family (*Hemerocallis*; Dahlgren et al. 1985) The evidence for this unsuspected alliance is from *rbcL* sequence analyses (Chase et al., 1995a), as well as palynological (Kosenko, 1994) and serological evidence (Chupov, 1987). *Xeronema* Brongn. & Gris, included by Clifford et al. (1998) has since been recognized as a monogeneric family (Xeronemataceae; AGP 1998), while the affinities of *Eccremis* Willd. ex Bak. may lie with Iridaceae (Rudall et al. 1996). Hemerocallidaceae is allied with Asphodelaceae and Xanthorrhoeaceae.

*Hyacinthaceae*. This family has been recognized as a natural group within Liliaceae *sensu lato* on the basis of anatomical (Fuchsig 1910) and embryological (Schnarf 1929; Wunderlich 1937; Buchner 1948) characters. Speta (1998) recognizes about 67 genera and 900 species in the family, subdivided into five subfamilies of which four are well-supported by molecular data (Chase et al. 1995; Fay and Chase 1996).

Molecular systematic work in progress (J. Manning pers. comm.) favors a more conservative circumscription of genera than that introduced by Speta (1998). Important horticultural genera include *Eucomis* L' Hér., *Hyacinthus* L., *Lachenalia* Jacq. F. ex Murray, *Muscari* Mill., *Ornithogalum* L., *Scilla* L., and *Veltheimia* Gled. Hyacinthaceae is allied with Themidaceae and Aphyllanthaceae (Fay and Chase 1996; Fay et al. 2000).

*Iridaceae*. Dahlgren et al. (1985) classified the iris family in Liliales near Colchicaceae on the basis of their extrorse anthers, non-phytomelanous seeds, mottled tepals, perigonal nectaries and nuclear endosperm development. Perigonal nectaries are now known to represent an independent, derived state in Iridaceae, as are mottled tepals, and septal nectaries are the ancestral state for the family (Goldblatt 1998). The more ancestral Iridaceae are characterized by helobial endosperm formation. Despite the lack of clear cut morphological links to Asparagales, multiple gene sequence analyses place Iridaceae well within this order (Chase et al. 1995a, 2000; Fay et al. 2000). The family occupies an isolated position among the well-resolved clades of the asparagoids, and probably represents a relatively ancient divergence from the rest of the order (Goldblatt 1998). Three subfamilies are recognized by Goldblatt (1998): Isophysidoideae (1 genus, Tasmania), Nivenioideae (7 genera, Australia, South Africa and Madagascar, three with woody aerial stems), Iridoideae 27 genera, cosmopolitan) and Ixioidae (27 genera, mostly African).

## CONCLUSIONS

Our current understanding of the relationships among the monocotyledons represents a quantum leap over the knowledge of just a few decades ago. New data continue to accumulate at an ever-increasing rate. Within the Asparagales, a precise understanding of the relationships among the basal, "lower" families is still elusive (Chase et al. 2000; Fay et al. 2000). Within Liliales, the relationships among the component families appear more resolute (Rudall et al., 2000), but the exact affinities of *Calochortus*, the relationships of Alstroemeriaceae, and the accurate alignment of the genera formerly treated as Uvulariaceae, remain to be further elucidated. Finally, the exact relationships among the lilioid orders Asparagales, Dioscoreales, Liliales and Pandanales (Fig. 1) are not yet well-resolved.

## Literature Cited

- Aagesen, L. and Sanso, A.M. 1998. Phylogeny of Alstroemeriaceae. Monocots II, 2<sup>nd</sup> international symposium on the comparative biology of the monocotyledons, Sydney, Australia (poster).
- Arroyo, S.C. and Cutler, D.F. 1984. Evolutionary and taxonomic aspects of the internal morphology in Amaryllidaceae from South America and Southern Africa. Kew Bull. 39:467-498.
- Angiosperm Phylogeny Group [APG; K. Bremer, M. W. Chase and P. Stevens, eds.]. 1998. An ordinal classification for the families of flowering plants. Ann. Missouri Bot. Gard. 85:531-553.
- Bayer, E. 1998. Alstroemeriaceae. In: K. Kubitzki, ed., The families and genera of vascular plants, vol. 3, flowering plants, monocotyledons, Liliales (except Orchidaceae), pp. 79-83, Springer-Verlag, Berlin.
- Buchner, L. 1948. Vergleichende embryologische Studien an Scilloideae. Österr. Bot. Z. 95:428-450.
- Caddick, L.R., Rudall P.J., Wilken P. and Chase M.W.. 2000. Yams and their allies: systematics of Dioscoreales. In: K. Wilson and D. Morrison, eds., Monocots: systematics and evolution., pp. 475-487, CSIRO Press, Sydney:
- Chase, M.W., Duvall, M.R., Hills, H.G., Conran, J.G., Cox, A.V., Eguiarte, L.E., Hartwell, J., Fay, M.F., Caddick, L.R., Cameron, K.M., and Hoot, S. 1995a. Molecular phylogenetics of *Lilianaes*. In: P.J. Rudall, P.J. Cribb, D.F. Cutler and C.J. Humphries, eds., Monocotyledons: systematics and evolution, pp. 109-137, Royal Botanic Gardens, Kew.

- Chase, M.W., Stevenson D.W., Wilkin P. and Rudall P.J.. 1995b. Monocot systematics: a combined analysis. In: P. J. Rudall, P.J. Cribb, D.F. Cutler and C.J. Humphries, eds., *Monocotyledons: systematics and evolution*, pp. 685-730, Royal Botanic Gardens, Kew.
- Chase, M.W., Soltis D.E., Soltis, P.S., Rudall, P.J., Fay, M.F., Hahn, W.H., Sullivan, S., Joseph, J., Molvray, M., Kores, P.J., Givnish, T.J., Sytsma, S.J. and Pires, J. Chris. 2000. Higher-level systematics of the monocotyledons: an assessment of current knowledge and a new classification. In: K. Wilson and D. Morrison, eds., *Monocots: systematics and evolution*, pp. 3-16, CSIRO Press, Sydney.
- Chupov, V.S. 1987. Taxonomic position of the genera *Geitonoplesium* and *Simethis*. *Bot. Zh. (Moscow)* 72:904-908.
- Clifford, H.T., Henderson, R.J.F. and Conran, J.G.. 1998. Hemerocallidaceae. In: K. Kubitzki, ed., *The families and genera of vascular plants*, vol. 3, flowering plants, monocotyledons, Liliaceae (except Orchidaceae), pp. 245-253, Springer-Verlag, Berlin.
- Conran, J.G. and Tamura, M.N. 1998. Convallariaceae. In: K. Kubitzki, ed., *The families and genera of vascular plants*, vol. 3, flowering plants, monocotyledons, Liliaceae (except Orchidaceae), pp. 186-198, Springer-Verlag, Berlin.
- Dahlgren, R.M.T. and Clifford, H.T. 1982. *The monocotyledons: a comparative study*. Academic Press, London.
- Dahlgren, R. and F.N. Rasmussen. 1983. Monocotyledon evolution: characters and phylogenetic analysis. *Evol. Biol*: 16:255-395.
- Dahlgren, R.M.T., Clifford, H.T. and Yeo, P.F. 1985. *The families of the monocotyledons*. Springer-Verlag, Berlin.
- Duvall, M.R., Clegg, M.T., Chase, M.W., Clark, W.D., Kress, W.J., Hills, H.G., Eguiarte, L.E., Smith, J.F., Gaut, B.S., Zimmer, E.A. and Learn, Jr G.H.. 1993. Phylogenetic hypotheses for the monocotyledons constructed from *rbcL* data. *Ann. Missouri Bot. Gard.* 80:607-619.
- Fay, M.F. and Chase, M.W. 1996. Resurrection of Themidaceae for the Brodiaea alliance, and recircumscription of Alliaceae, Amaryllidaceae and Agapanthoideae. *Taxon* 45:441-451.
- Fay, M.F., Rudall, P.J., Sullivan, S., Stobart, K.L., de Bruijn, A.Y., Reeve, G., Qamaruz-Zaman, F., Hong, W.-P., Joseph, J., Hahn, W.J., Conran, J.G. and Chase M.W. 2000. In: K. Wilson and D. Morrison, eds., *Monocots: systematics and evolution*, pp. 360-371, CSIRO Press, Sydney.
- Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39:783-791.
- Felsenstein, J. 1988. Phylogenies from molecular sequences: inference and reliability. *Ann. Rev. Genetics* 22: 521-565.
- Fuchsig, H. 1911. Vergleichende Anatomie der Vegetationsorgane der Lilioideen. *Sitzungsber. Kais. Akad. Wiss. Wien, Math.-Naturw. Kl.* 120: 1-43, I-III.
- Goldblatt, P. 1995. The status of R. Dahlgren's orders Liliales and Melanthiales. In: P.J. Rudall, P.J. Cribb, D.F. Cutler and C.J. Humphries, eds., *Monocotyledons: systematics and evolution*, pp. 181-200, Royal Botanic Gardens, Kew.
- Goldblatt, P. 1998. Iridaceae. In: K. Kubitzki, ed., *The families and genera of vascular plants*, vol. 3, flowering plants, monocotyledons, Liliaceae (except Orchidaceae), pp. 295-333, Springer-Verlag, Berlin.
- Hennig, W. 1966. *Phylogenetic systematics*. Univ. Illinois Press, Urbana.
- Hillis, D.M. and J.J. Bull. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Syst. Biol.* 42: 182-192.
- Huber, H. 1969. Die Sammenmerkmale und Verwandtschaftsverhältnisse der Liliiflorae. *Mitt.Bot. Staat. München* 8:219-538.
- Hutchinson, J. 1934. *Families of flowering plants*, vol. 2, monocotyledons, 1st ed. MacMillan and Co., London.
- Ito, M., Kawamoto A., Kita Y., Yukawa T. and Kurita S. 1999. Phylogeny of



- Amaryllidaceae based on *matK* sequence data. Jap. J. Plant Res. 112:207-216.
- Kosenko, V.N. 1994. Morfologiya pyl'tsy semeistv Phormiaceae, Blandfordiaceae I Doryanthaceae. Bot. Zh. 70:1-12.
- Kubitzki, K. (ed.). 1998. Families and genera of vascular plants, flowering plants, monocotyledons, Liliaceae (except Orchidaceae). Springer-Verlag, Berlin.
- Meerow, A.W. 1995. Towards a phylogeny of the Amaryllidaceae. In: P.J. Rudall, P.J. Cribb, D.F. Cutler and C.J. Humphries, eds., Monocotyledons: systematics and evolution, pp. 169-179, Royal Botanic Gardens, Kew.
- Meerow, A.W. and Snijman, D.A. 1998. Amaryllidaceae. In: K. Kubitzki, ed., The Families and Genera of Vascular Plants. Vol. 3. Flowering Plants. Monocotyledons. Liliaceae (except Orchidaceae), pp. 83-110, Springer-Verlag, Berlin.
- Meerow, A.W., Fay, M.F., Guy, C.L., Li, Q.-B., Zaman, F.Q. and Chase, M.W. 1999. Systematics of Amaryllidaceae based on cladistic analysis of plastid *rbcL* and *trnL-F* sequence data. Amer. J. Bot. 86:1325-1345.
- Meerow, A.W., Fay, M.F., Chase, M.W., Guy, C.L., Li, Q.-B., Snijman, D. and Yang, S.-Y. 2000a. In: K. Wilson and D. Morrison, eds., Monocots: systematics and evolution., pp. 372-386, CSIRO Press, Sydney.
- Meerow, A.W., Guy, C.L., Li, Q.-B. and Yang, S.-Y. 2000b. Phylogeny of the American Amaryllidaceae based on nrDNA ITS sequences. Syst. Bot.: in press.
- Müller-Doblies, D. and Müller-Doblies, U. 1996. Tribes and subtribes and some species combinations in Amaryllidaceae J. St.-Hil. emend. R. Dahlgren et al. 1985. Feddes Rep. 107: S.c. 1-9.
- Nordenstam, B. 1998. Colchicaceae. In: K. Kubitzki, ed., The Families and Genera of Vascular Plants. Vol. 3. Flowering Plants. Monocotyledons. Liliaceae (except Orchidaceae), pp. 175-185, Springer-Verlag, Berlin.
- Patterson, T.B. and Givnish, T.J. 1998. Phylogeny and evolutionary trends in Liliaceae s.s., Calochortaceae and Uvulariaceae: insights from *ndhF* sequence data. Amer. J. Bot. 85 (suppl.):149-150 (Abstract).
- Rahn, K. 1998. Alliaceae. In: K. Kubitzki, ed., The families and genera of vascular plants, vol. 3, flowering plants, monocotyledons, Liliaceae (except Orchidaceae), pp. 70-78, Springer-Verlag, Berlin.
- Rudall, P.J., Cribb, P.J., Cutler, D.F. and Humphries, C.J., eds. 1995. Monocotyledons: systematics and evolution. Royal Botanic Gardens, Kew.
- Rudall, R.J., Chase, M.W. and Conran, J.G. 1996. New circumscriptions and a new family of asparagoid lilies: genera formerly included in the Anthericaceae. Kew Bull. 51:667-680.
- Rudall, P.J., Furness, C.A., Chase, M.W. and Fay, M.F.. 1997. Microsporogenesis and pollen sulcus type in Asparagales (Liliaceae). Can. J. Bot. 75:408-430.
- Rudall, P.J., Stobart, K.L., Hong, W-P, Conran, J.G., Furness, C.A., Kite G.C. and Chase, M.W. 2000. Consider the lilies: systematics of Liliales. In: K. Wilson and D. Morrison, eds., Monocots: systematics and evolution., pp. 347-359, CSIRO Press, Sydney.
- Sanderson, M.J. 1989. Confidence limits on phylogenies: the bootstrap revisited. Cladistics 5:113-129.
- Schnarf, K. 1929. Die Embryologie der Liliaceae und ihre systematische Bedeutung. Sitzungsber. Kais. Akad. Wiss. Wien, Math.-Naturw. Kl. 138, Abt. I:69-92.
- Speta, F. 1998. Hyacinthaceae. In: K. Kubitzki, ed., The families and genera of vascular plants, vol. 3, flowering plants, monocotyledons, Liliaceae (except Orchidaceae), pp. 261-285, Springer-Verlag, Berlin.
- Stevenson, D.W. and Loconte, H. 1995. Cladistic analysis of monocot families. In: P. J. Rudall, P.J. Cribb, D.F. Cutler and C.J. Humphries, eds., Monocotyledons: systematics and evolution, pp. 685-730, Royal Botanic Gardens, Kew.
- Tamura, M.N. 1998a. Calochortaceae. In: K. Kubitzki, ed., The families and genera of vascular plants, vol. 3, flowering plants, monocotyledons, Liliaceae (except Orchidaceae), pp. 164-172, Springer-Verlag, Berlin.

- Tamura, M.N. 1998. Liliaceae. In: K. Kubitzki, ed., The families and genera of vascular plants, vol. 3, flowering plants, monocotyledons, Liliaceae (except Orchidaceae), pp. 343-353, Springer-Verlag, Berlin.
- Tamura, M.N. 1998c. Melanthiaceae. In: K. Kubitzki, ed., The families and genera of vascular plants, vol. 3, flowering plants, monocotyledons, Liliaceae (except Orchidaceae), pp. 369-380, Springer-Verlag, Berlin.
- Tamura, M.N. 1998d. Trilliaceae. In: K. Kubitzki, ed., The families and genera of vascular plants, vol. 3, flowering plants, monocotyledons, Liliaceae (except Orchidaceae), pp. 444-452, Springer-Verlag, Berlin.
- Traub, H.P. 1963. Genera of the Amaryllidaceae. American Plant Life Society, La Jolla, CA.
- Wiley, E.O. 1981. Phylogenetics, the theory and practice of phylogenetic systematics. John Wiley and Sons, New York.
- Wilson, K. and Morrison, D. eds. 2000. Monocots: systematics and evolution. CSIRO Press, Sydney.
- Wunderlich, R. 1937. Zur vergleichenden Embryologie der Liliaceae-Scilloideae. Flora 132:48-90.
- Zomleffer, W.B. 1996. The Trilliaceae in the southeastern United States. Harvard Pap. Bot. 9:91-120.
- Zomleffer, W.B. 1997. The genera of Melanthiaceae in the southeastern United States. Harvard Pap.Bot. 2:133-177.

## Figures

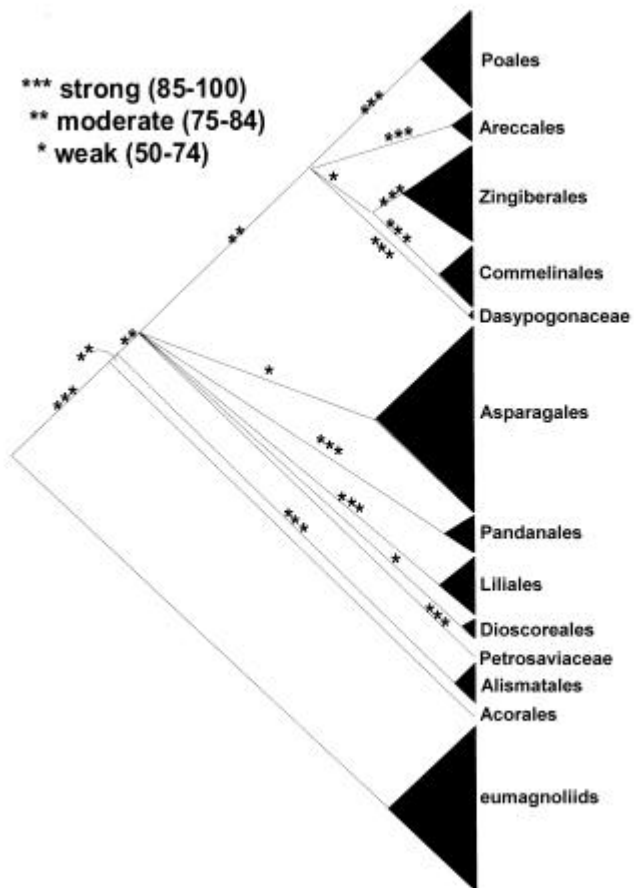


Fig. 1. Ordinal relationships of the monocotyledons based on a three gene sequence data matrix (Chase et al., 2000). Asterisks indicate degree of bootstrap support. Reprinted with permission of author.

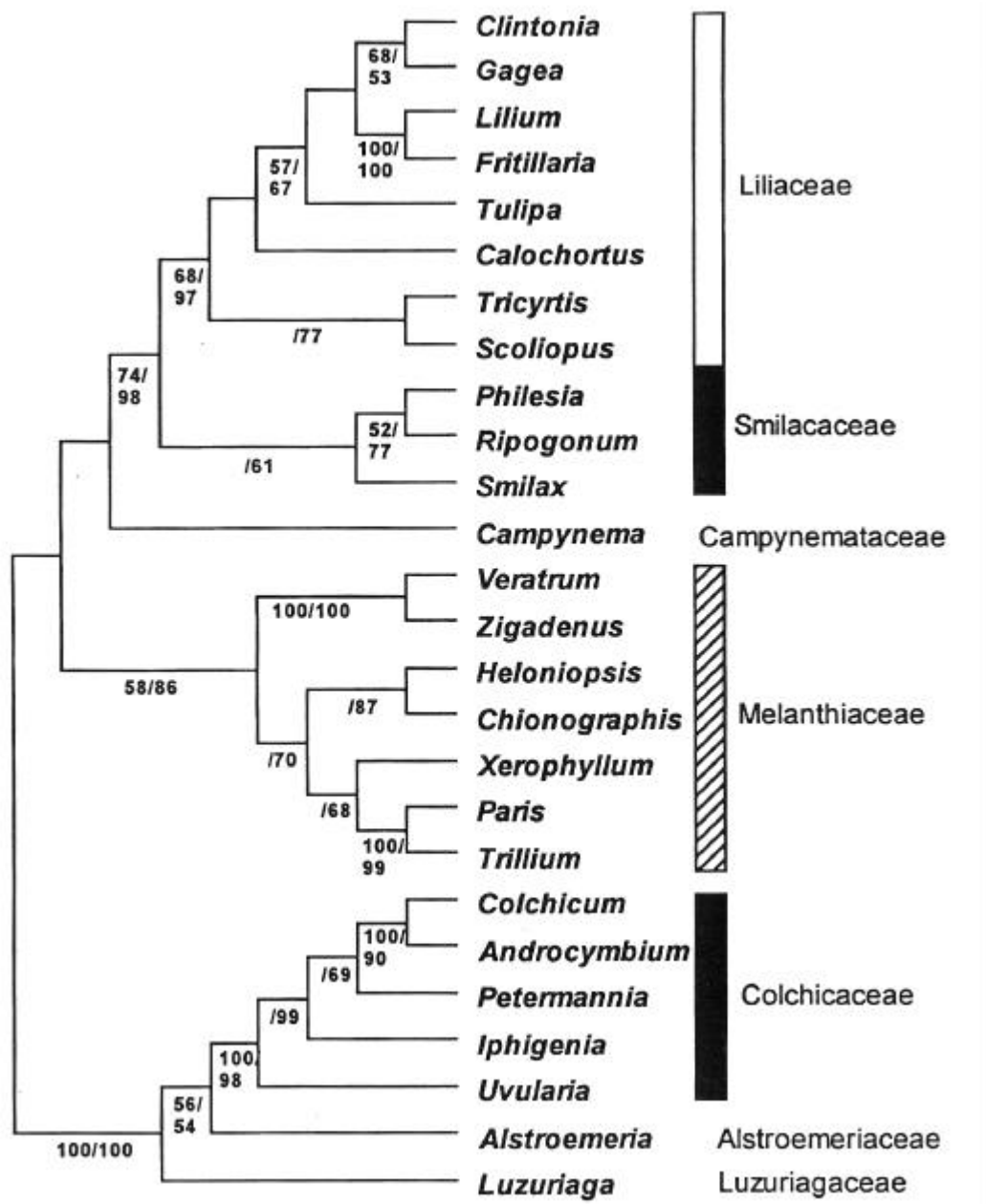


Fig. 2. Strict consensus tree for genera of Liliales produced by combined analysis of morphological and plastid *rbcL* and *trnL-F* sequence data (Rudall et al. 2000). Numbers represent bootstrap values for molecular/combined trees. Reprinted with permission of author.

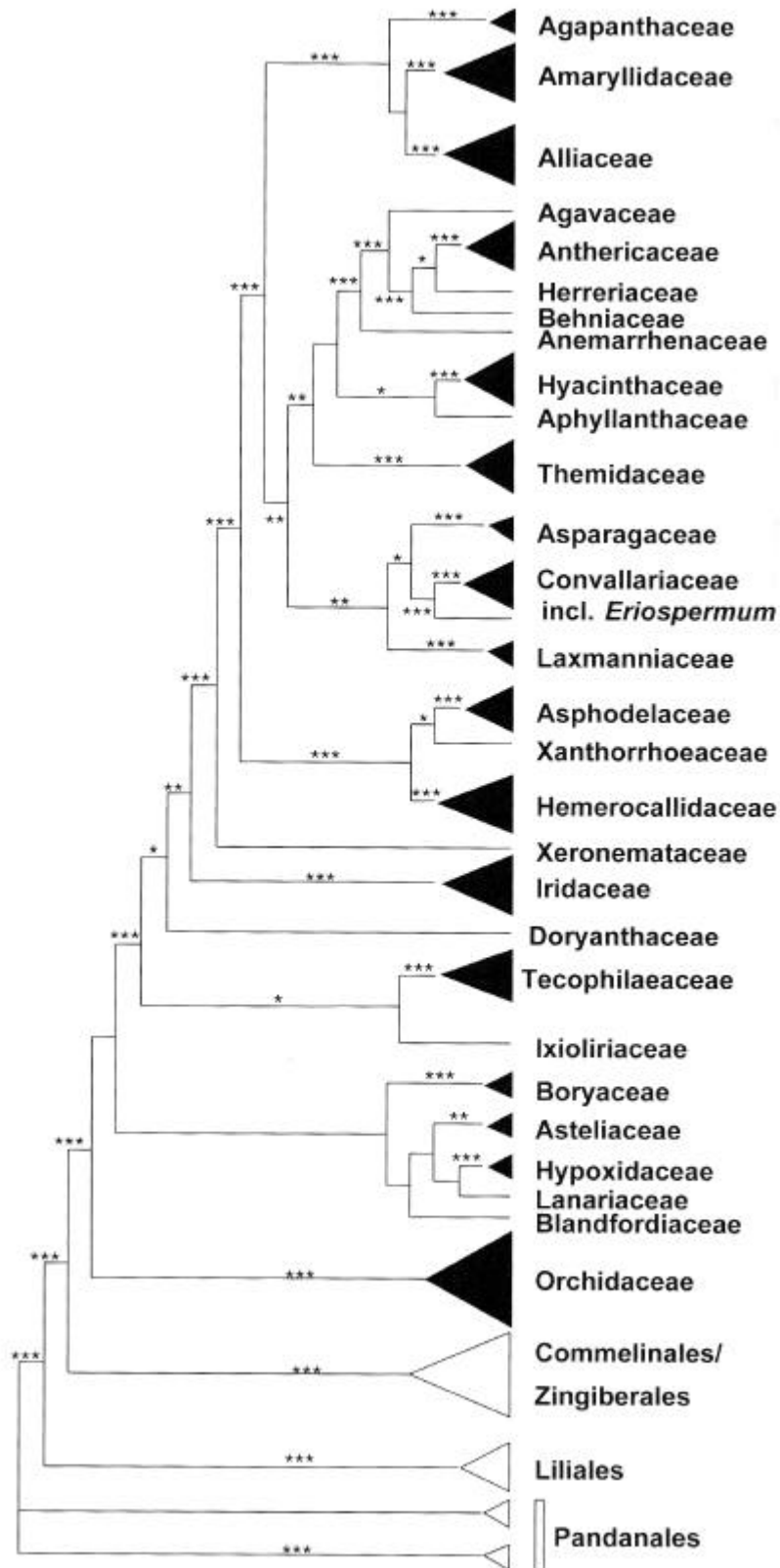


Fig. 3. Single most parsimonious tree obtained from analysis of Asparagales with four plastid DNA sequences (Fay et al., 2000). Asterisks indicate degree of bootstrap support: \*\*\* = 90-100%, \*\* = 80-89%, \* = 65-79%. Reprinted with permission of author.

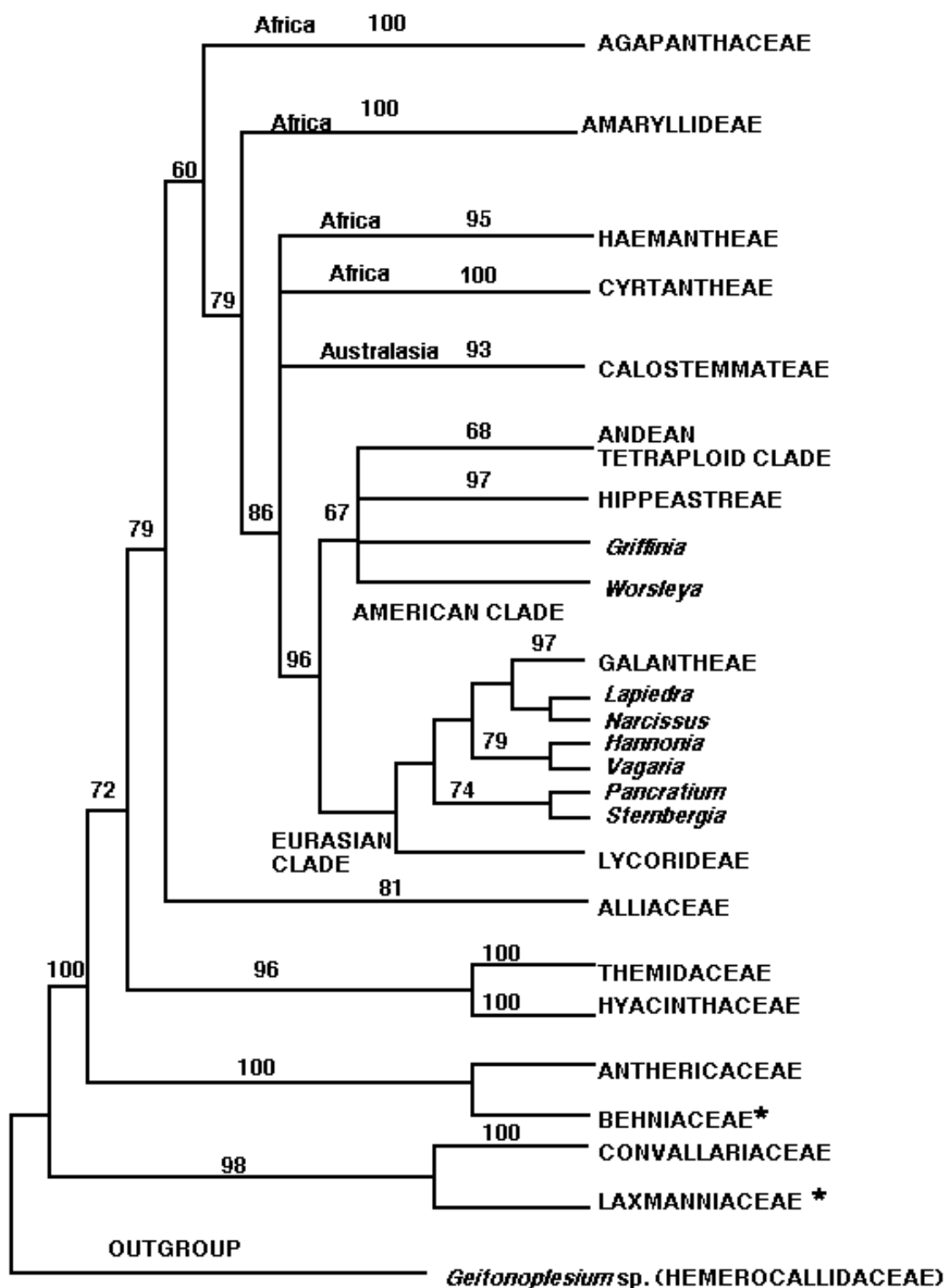


Fig. 4. Strict consensus of 5000 equally parsimonious trees generated by cladistic analysis of successively weighted combined *rbcL* and *trnL-F* sequence matrix for Amaryllidaceae and other Asparagalean genera (Meerow et al. 2000a). Numbers above branches are bootstrap support percentages. Geographic position of major clades is indicated. An asterisk after a terminal taxon indicates that a single species was used as an exemplar in the analysis.

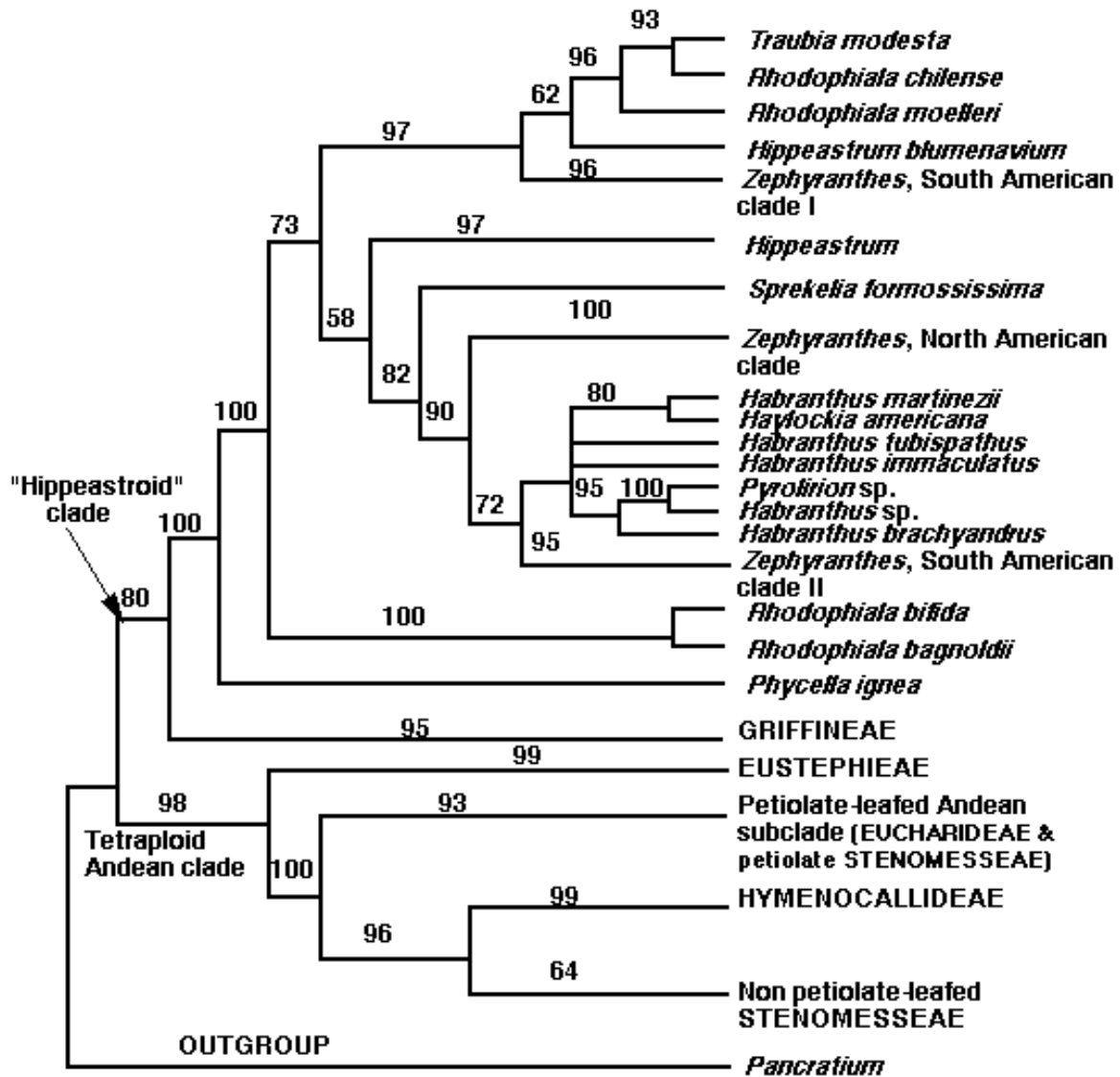


Fig. 5. Strict consensus of 2699 equally most parsimonious trees generated by cladistic analysis of successively weighted nuclear ribosomal DNA ITS sequence matrix with binary gap matrix included for American Amaryllidaceae (Meerow et al. 2000a, b). Numbers above branches are bootstrap support percentages.